FIELD BEHAVIOR AND SOUND PRODUCTION BY THE GRASSHOPPER SPHINGONOTUS RUBESCENS (ORTHOPTERA: ACRIDIDAE) ON TENERIFE, CANARY ISLANDS¹

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ABSTRACT: Males and females of the oedipodine grasshopper *Sphingonotus rubescens* crepitate by producing a click-buzz sound. Males have 3 types of stridulation: (1 and 2) a common whistle-click combination lasting less than 1 sec and often followed by a hop-turn or very short flight, and (3) a buzzing lasting ca. 1/2 sec when 2 or more males are less than 1 m apart. Male courtship behavior is described.

Sphingonotus rubescens (Walker) is an ubiquitous oedipodine grasshopper generally found below 300 m in the desert sublittoral scrub zone along the coastline of Tenerife, one of the Canary Islands (Holzapfel 1970, Gangwere 1972). It also occurs in Afro-Asia, India and the Mediterranean (Mistshenko 1936). This paper reports on field observations of adult *S. rubescens* habitats, behavior and sound production during the unusually dry winter and spring seasons of Tenerife in 1975.

Tenerife is a 2,057 km², subtropical, volcanic island with a narrow precipitous coastline and central mountain range. The mountains, rising to 3,716 m above sea level, extend the length of the island. The coastal scrub zone is windy, hot, and dry whereas the more humid northern coastal zone has more rainfall, lush vegetation and is covered by low clouds during the summer. The mountains support laurel and pine forests, a subalpine scrub zone and alpine barrens. Of the nearly 2,000 plant species on Tenerife, approximately 91 are endemic (Lems 1960). There are 28 species of acridoids and 2 are endemic (Gangwere et al. 1972).

The genus Sphingonotus consists of slightly over 100 species and subspecies (Mistshenko 1936, Huang 1982) but only 5 occur on Tenerife (Holzapfel 1970, Gangwere et al. 1972). Although there is some taxonomic confusion as to whether S. rubescens is in reality the same as S. caerulans (L.) (= coerulans) on Tenerife (Holzapfel 1970), all but 2 of the hundreds of individuals I observed or collected conformed to the description of S. rubescens in the keys of Holzapfel (1970) and Johnsen (1974) and generally matched the description by Mistshenko (1936). Essentially it is a dull brownish-gray grasshopper with occasional brown or reddish-brown color variants that tend to match the soil color. The tegmina have fascia and/or spots and the hindwings are clear. The basal half of the hindwings of

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the 2 nonconforming specimens were pale blue and the individuals appeared to be *S. caerulans* based on Holzapfel's key (1970). One was captured in a coastal scrub zone and the other in the pine forest zone at ca. 1500 m near Vilaflor. A third species, *S. savignyi* Saussure, was collected in small numbers in very localized pumice and outwash plains near El Medano.

METHOD OF STUDY

I observed grasshoppers in the field by remaining inanimate for long periods of time in their habitat until normal activity resumed. A stopwatch was used to time specific behavior. Individuals were also confined in an 8 liter aquarium with an incandescent light placed above. However, behavior was relatively subdued under these conditions resulting in a minimal amount of useful data.

Habitat: The habitats most frequented by the geophilous *S. rubescens* are flat, sandy, dry river beds, outwash plains, fields of small, gray pumice and crushed rock, and vacant sandy or gravely sites between widely-spaced buildings in villages along the western and southern coasts. Gravel, pebbles and sometimes rocks up to 9 cm across are strewn abundantly across these sites and often the greatest number of *S. rubescens* $(0.1 - 0.3/m^2)$ occurs in areas containing the most rubble. The population density more commonly averaged 1 grasshopper/125 m² in habitats where the species occurred. Nymphs were rarely observed during the collecting periods of January to May.

Common plants in these xeric habitats include sparse growths of *Nicotiana glauca* Graham (Solanaceae), *Beta patellaris* Moq. (Chenopodiaceae), and *Mesembryanthemum crystallinum* L. (Aizoaceae), and several species of unidentified grasses growing in patches. *S. rubescens* may also be collected on old hillside terraces of sandy, reddish-brown volcanic soils containing pumice 2 to 9 cm in size scattered at densities up to 100/m². Vegetation is very sparse on the terraces during the dry winter and spring and consists of short, dry grasses and occasional *Euphorbia* and *Opuntia* spp.

Grasshoppers were more likely to occur between clumps of vegetation rather than on or in vegetation. During the evening they moved into grass and debris or sought shelter under rocks. Individuals were observed to feed on dead grass blades on the ground, dead leaves of *B. patellaris*, and green leaves of *Calendula arvensis* L. (Compositae) growing at 1500 m elevation. Adults survived in captivity on *C. arvensis* leaves, flowers, and stems up to 50 days and one female oviposited 26 eggs on the side of the container.

Crepitation: S. rubescens flights (n = 25) are 0.5 to 2 m above the ground and cover a distance of 3 to 9 m for males and up to twice this distance for the larger females. Flight time ranges from 1.5 to 6 sec for males. There is no hovering or display by this clear-winged species. Crepitation begins about 1 sec prior to landing when the male produces a single-pulse "click" sound which is immediately followed by a "buzz," each portion lasting 1/3 to 1/2 sec. The more active males crepitate commonly and females are occasionally heard. Male flights with crepitation may bring the male closer to a male or female, but the same grasshopper might also fly again a few minutes later to a site more distant from other grasshoppers without any interaction having occurred. Crepitation did not serve as a male aggregating signal. S. rubescens will also crepitate due to human disturbance. Johnsen (1972) reported that the tegmen of S. rubescens has a raised longitudinal ridge that grips the costa of the hind wing. When the tegmen is manipulated upward it releases the costa which causes an audible click. The mechanism causing the buzz is unknown.

Stridulation: Three non-graded types of stridulation occur in the Oedepodinae (Otte 1970): ordinary and vibratory stridulation and ticking. Stridulation by male S. rubescens approximates these 3 types. The louder and more common sounds (ordinary stridulation and ticking) are heard from males widely scattered (usually more than 5 m apart) on the ground or on small rocks. The presence or absence of nearby females seems to have no effect on the initiation or continuation of the sounds which suggests that they are calling rather than courtship signals, since pair formation has not yet occurred. The male simultaneously rubs both hind legs against the tegmina and rapidly vibrates his body from side to side. He may also move several cm forward on his front and middle legs while stridulating. The sound consists of a soft, high-pitched "wheet-wheet" (2-pulse whistle) lasting about 1/2 sec. A single "wheet" increases in pitch by ca. 1^{1/2} octaves (estimation by ear) between initiation and termination. The whistle is typically followed by ticking which consists of 4 rapid ticks (i.e., clicks) lasting a total of ca. 2/3 of the whistle's duration. A short burst of activity usually follows the whistle-ticking combination and consists of (1) a 1-cm or less hop followed by a 15 to 45° turn in a seemingly random direction and then a forward movement of ca. 1 cm or (2) an occasional short flight of ca. 1 m.

The closest approximation of the whistle may be made manually by rubbing the spined inner side of the hind tibia against the area (flap) bounded by the intercalary vein and the leading edge of the tegmen. This flap flexes near the intercalary vein when displaced by tibial spines. Johnsen (1972) also noted this whistle but believed that is is caused by tegmino-femoral stridulation. However, my observations indicate that the femur may not be involved in this particular sound production since the tibia can be manipulated to mimic the whistle and the femur's inner surface bows slightly outward causing it to miss the wing flap.

To produce a tick rather than a whistle, the tibia is not brought up as high or as far forward as it rubs against the tegmen. Johnsen (1972) theorized that the ticking (his "kneck-kneck" sounds) is caused by a tegmino-alar mechanism because the tegmen has a longitudinal ridge on its inner surface which may grip and then release the hindwing. When manipulated upward the tegmen produced the "kneck" sound. I was unable to detect tegmino-hindwing movements during ticking, whereas the hind legs always vibrated indicating the tegmino-tibial opposition is more likely the cause of this sound. Otte (1970, 1972) noted that ticking is caused by the tibia striking the end of the tegmen in some oedipodines that he studied in No. America and Australia. In these cases the ticking was usually part of courtship behavior. Haskell (1957) also commented on repetitive clicks during courtship in a common European acridine. In the case of *S. rubescens* ticking is part of the calling signal and a component of courtship.

The third type of stridulation involves male-male interaction (aggression) when two males are within ca. 0.6 m of each other. One individual initiates a soft buzzing sound (vibratory stridulation) lasting about 1/2 sec as both hind legs move rapidly up and down. The femur appeared to be rubbing against the tegmen but the sound could not be duplicated by hand manipulation. The buzzing may be followed by a rapid forward movement of ca. 1 cm in the general direction of the second grasshopper. Within seconds after completion of the stridulation by the first male, the second individual repeats the sound and movement which are then repeated by the first male. As many as 5 repetitions were recorded for each grasshopper and one or both males may wander up to 30 cm during a group of repetitions. There is a silent period of 30 sec to 5 min ($\bar{x} = 1.5$ min) between groups of repetitions and some femur-tipping occurs during this time. On one occasion a third male approached and for about 1 min a three-way communication occurred although an individual's buzzing would sometimes overlap another's. There is no contact between males and they eventually disperse by walking or flying.

Buzzing has been heard in various acridines (e.g., *Arphia* spp. in No. America) during various male-female encounters (Willey and Willey 1969, Otte 1970). Male chorusing has been reported in European Acridinae (Haskill 1957) and certain No. American Oedipodinae (Otte 1970).

Stridulatory activity was also observed during male-female pair formation although copulation was rarely encountered during the winter period. The following example of courtship behavior is typical of the 5 male-female interactions observed, where the male eventually attempts to copulate with an unreceptive female. The female was foraging by crawling on soil and rocks and periodically stopping for several minutes to bask in the sun. A male was following ca. 30 cm away and every 1 to 2 min he made the common "wheet-wheet" (whistle) sound followed by 4 to 9 ticks. He followed the female for 3 m and although he would lose sight of her behind a rock on occasions, he made no immediate effort to move closer and relocate her. Each short walking period on the ground was preceded by the whistle-tick combination or, rarely, 2 to 3 ticks without a whistle. In the latter case, observations of other males showed that as the male approached to within 4 to 5 cm the number of ticks increased to 4 or more and were then preceded by the usual whistle.

After nearly 15 min had pased the male approached the female several times to within 2 to 3 cm. His antennae began slowly waving synchronously and when he was close to making contact (but did not) and still stridulating, the female kicked at him with a hind tibia forcing him to back up 5 to 8 cm. He made two half-circles around the female while stridulating and then continued following behind her or moved parallel to or ahead of her until she again kicked at him. Attempted mounting of males on females is almost always from the side. After several retreats he maintained a 10 to 15 cm distance from the female. She made no sound nor any femur-raising or femur-vibration movements during the 20 min observation and finally went out of his sight behind a rock. The male made a few whistle-ticks during the next few minutes but did not follow and finally settled into a shallow concavity on top of a rock.

DISCUSSION

Communicative behavior has been studied with only a few species of *Sphingonotus* (Faber 1936, Jacobs 1953, Uvarov 1966, Otte 1972). *S. erythropterus* Sjöst, an Australian species, has hindwings and inside femoral surfaces that are bright orange and a simple repetoire of courtship sequences (Otte 1972). *S. savignyi*, an African species also found on Tenerife, lacks colorful wings but has light or dark contrasting body markings. It utilizes three methods of sound production: wing crepitation, rubbing the tegmen against the hindwing, and rubbing the femur against the tegmen (Uvarov 1966). *S. caerulans*, a European species apparently confused with *S. rubescens* on the Canary Islands, has pale blue wings but, unlike *S. rubescens*, it does not have a crepitation display (Faber 1936, Jacobs 1953). Although males produce trill-whistle sounds very similar to those of *S. rubescens*, Faber (1936) and Jacobs (1953) do not mention any associated ticking sounds.

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I recently observed the legs and wings of *S. rubescens* with a scanning electron microscope. The femora have a non-serrated, acute scraper ridge but the tibial spines have no surface modifications that might indicate any unusual sound-producing ability. No serrated veins were present on the hindwings and only the intercalary veins of the tegmina were serrated. The non-articulated teeth on the veins of males averaged 3 μ m high and 30 μ m apart. They appear nearly identical to the intercalary teeth on the tegmina of *S. caerulans* illustrated by Jacobs (1953).

S. rubescens lacks morphological specializations to enhance visual and audio signals. For instance, although it crepitates, the wings are clear rather than brightly colored. The inner surface of the femora has 2 pale bands which are inconspicuous when femur-raising occurs. The anal veins of the hindwing are not unusually thickened which otherwise have been shown to produce a loud chorus in a few oedipodine species (Otte 1970). The whistle, ticking and buzzing sounds of males with the associated body movements are not unusually complex for oedipodines but apparently convey sufficient signals to ensure male-female interaction.

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